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THE BOTANICAL REVIEW

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CYTOLOGY AND GENETICS OF BARLEY[1]

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INTRODUCTION

This résumé is an attempt at a comprehensive review of the literature on cytological and genetic investigations concerning one of the most important plants from the standpoint of history, agriculture and science. A glance at the list of authors at the end of this article will reveal that hundreds of scholars have made contributions to the sum of knowledge regarding barley, though many investigators have used the plant because of certain advantages which it has as a subject for research rather than because they were interested in the plant itself.

There are two chief differences between the literature on barley and the literature dealing with the cytogenetics of wheat (2, 3). In the first place, comparatively few specific and generic crosses with barley have been made. In the second place, because of the small number of chromosomes and the large number of clearly classifiable characters, barley is among the top half-dozen plant species in the number of gene loci plotted on linkage maps.

The literature also shows that barley has been a favorite species for studies on methods of experimentally modifying heredity, particularly in the field of irradiation.

About 1400 articles have been perused in preparing this review, of which over 900 are listed in the Bibliography. Many hundreds more have been written which did not seem from their titles to deal directly with the subject being reviewed. Takahashi (778) estimated that over 1300 articles had been published on barley up to 1941. He listed about 1275 papers, grouped as follows: *a*) general, morphology, classification, etc.: 171; *b*) genetics, cytology and plant breeding: 344; *c*) diseases, including genetics of disease resistance and varietal response: 148; *d*) physiology and cultivation: 487; *e*) brewery, chemical and physical properties of grain: 124. The following were also especially fruitful sources of citations: Agricultural Index, Bibliography of Agriculture, Biological Abstracts, Botanical Abstracts, Experiment Station Record, Plant Breeding Abstracts, and references 120, 320, 518, 676, 677, 749 and 873.

The writer feels that the bibliography is reasonably complete, but there may be serious omissions. Perhaps, also, errors in interpretation of experimental results have been made. He would

appreciate having both types of imperfections called to his attention. Receipt of reprints of papers on barley already published, or published in the future, will be welcomed.

For brevity, author's license has been taken in many instances in this review. For example, "characters" are spoken of as being "inherited", but the reader will understand that it is meant that the genes for characters are inherited. The reader will likewise understand that a character is not the result of the action of a single gene, but rather of one gene in cooperation with all the other genes of the organism in a given environment.

In speaking of treated material (e.g., X-rayed, mustard-gas-treated), "X_1", "M_1", etc., have been used to designate plants grown from the treated seeds; "X_2", "M_2", etc., for offspring of plants grown from treated seeds. Furthermore, it should be understood that there is an appreciable spontaneous mutation (or aberration) rate and that any given change may not have been the result of experimental treatments. However, to save words, the writer refers to specific mutations, etc., as "induced".

Unless otherwise indicated, the observations reviewed here were made on forms of common barley (section Cereale). Therefore, for brevity, in most cases the word "barley" is omitted.

References which for one reason or another are not listed in the main bibliography are added at the end of that bibliography—under Appenda. Not all of these added titles are referred to in the text. Those that are referred to are cited by the author's name and the year of publication followed by the letter "A"—e.g., Smolak (1926A)—instead of by number only.

BARLEY AS AN EXPERIMENTAL PLANT

Origin

According to Vavilov (855), there are two main centers of diversity of barley. One, pivoting around Abyssinia and North-Eastern Africa, is particularly rich in long-awned hulled forms. The other, centering in China, Japan and Tibet, is the source of hull-less, short-awned, awnless or hooded types. Some workers consider *H. agriocrithon* E. Aberg and *H. spontaneum* C. Koch to be the progenitors of cultivated barleys. Vavilov observed that the area of diversity of *H. spontaneum* did not coincide with the two centers of diversity of cultivated types, but corresponded more

with the African. However, Nabelek (566) found *H. spontaneum,* consisting of three varieties, to be rather widespread in the Orient. The reader will find that many authors (7, 53, 226, 315, 399, 429, 605, 650, 702, 854, 855, 880, Covas 1950cA, and others) have made contributions to information on the origin of barley. A brief statement on the origin of barley as well as some history on barley culture was published by Weaver (1950A). Larionov (472) also presented observations on the phylogenetic relationship between two- and six-rowed barley.

Taxonomy and Cytology

SPECIES. Many taxonomists have worked on barley, and there are numerous disagreements, past and present, in barley systematics. Consequently there may appear to be contradictions in species names, etc., in this review. Aberg's (7) system of nomenclature has been selected arbitrarily for the Cereale section, although the reader may find the work of Beaven (53), Covas (1949A) and particularly that of Orlov (596) helpful in the identification of species and botanical varieties. About 25 species, divided into three or four sections, have been described. Only a few of the more recent publications dealing with the classification of species (7, 53, 122, 144, 311, 399, 575, 595, 596, 705, 891, Bergal 1948A, Covas 1949A, Schiemann 1949A) and agricultural varieties (10, 55, 311, 690, 891, Bergal and Friedberg 1940A) are listed in the bibliography. Reviews of and citations to earlier literature on taxonomy of barley may be found by consulting these references.

Aberg and Wiebe (10) and Orlov (596) described and illustrated a number of the characters used in taxonomic classifications of barley. Nakao (570, 1947A) suggested differences in nine morphological characters that could be used as a basis for identifying and classifying species and varieties. In some cases physiological characteristics (144) and biochemical reactions (781) have been used to differentiate types. Harlan (310) and Barbacki (49) made valuable contributions in describing the range of variation of a number of these varietal and species characters. Christie and Gran (133) found that climate had a distinct effect on earliness, number of culms and several other characters. Lorenz (497) and a number of others have studied variability within pure

lines of barley. Miege (534) also studied the variability of "varietal or taxonomic characters" of different spikes of the same plant, different plants of the same variety, and in different generations. Blaringhem (76) and others have shown that some of the "species characters" are simply inherited and easily separated from other characteristics of the same species.

CHROMOSOME NUMBERS. All cultivated species of barley have seven pairs of chromosomes. Among the wild forms, species with seven, 14 and 21 pairs occur. Different chromosome numbers have been reported for several species. Some of the disagreement may well result from confusion in the taxonomy. The species, their chromosome numbers and authorities for the counts are given in Table I.[2]

Summaries of reports on chromosome numbers of species and varieties may be found in papers by Gaiser (243–246), Tischler (821–825), Covas (144), Myers (563), Maude (519), Kihara, Yamamoto and Hosono (442), Yamamoto (902), and the book by Darlington and Ammal (148). Gaiser's summaries are especially complete, in some cases classifying the species into subgenera and sections (245). Literature citations in some of the other summaries, especially those of Tischler, are inconvenient.

The relation of number of chromosomes in species to length of life cycle has been considered (349, 552). Three annual species (*Caput medusae, maritimum* and *spontaneum*) had seven pairs of chromosomes; one (*jubatum*) had 14 pairs; and two (*murinum* and *gussoneanum*) had both seven- and 14-chromosome forms. Of the perennial species, three (*bulbosum, jubatum* and *silvaticum*) had 14 pairs; one (*nodosum*) had seven-, 14- and 21-chromosome forms; one (*secalinum*) had seven- and 14-chromosome forms.

Barley is one of the plants which Huskins and co-workers (376) are using in a critical study which may modify the accepted theory that somatic cells characteristically have the diploid number of chromosomes. They concluded that "differentiated cells—in roots of *Rhoeo* and *Hordeum* are normally polyploid or polytene".

CHROMOSOME MORPHOLOGY. Chromosomes of barley are comparatively large, seven to eight mu (254, 255, 256, 491), approxi-

[2] At the end of the third part of this article in the May issue.

mately the same size as those of wheat and considerably larger than those of maize in condensed phases (118). The ratio of the longest to the shortest chromosome was reported by Kagawa (418) to be 100:69 in *H. distichum* and 100:62 in *H. jubatum*. Lewitsky (491) obtained a ratio of 100:82 for length of the longest to shortest chromosomes of *H. distichum*.

All seven of the chromosomes of the cultivated species have median (255, 256, 494), sub-median (409, 418, 491) or subterminal to submedian (685) centromeres. Kagawa (418) observed one to three constrictions in chromosomes of *H. distichum* after treatment with chloral hydrate.

Of the seven chromosomes, two have satellites (118, 129, 254, 255, 258, 351, 409, 430, 491, 725, 830). Emme (174) reported that some varieties had no satellites, others had one, still others had two. Stählin (747) likewise reported none and one satellite in different varieties. Subsequent reports indicate that these observations were not accurate. Emme acknowledged that she had been shown satellites in barley by a Russian worker, Nikolajewa, who, so far as the writer is aware, did not report the finding. Ghimpu (253, 256) observed only one pair of satellited chromosomes, but they were present in each of the 14 species studied. Ruttle and Nebel (685) observed one pair of satellites, and Greis (274) also figured only one pair of satellited chromosomes in autotetraploid barley. Chin (129) observed that wild species with seven pairs of chromosomes had only one pair, and five 14-pair species had two pairs of chromosomes with satellites. In the figures of Perak (604) some species were illustrated as having satellites, while others were without. However, no point was made of the presence, absence or number of satellites. According to Covas (144), two pairs of chromosomes in tetraploid as well as diploid species have satellites.

One of the chromosomes has a large appendage that is sometimes set off by a prominent constriction (331). Thus evidently two pairs of chromosomes have satellites of different sizes (430, 491, 725), and a third pair has a still larger appendage. There is good reason to believe that by diligent work with already available technics, the seven chromosomes of cultivated barleys could be distinguished and identified with their respective linkage groups, as has been done with maize and *Drosophila*.

Ghimpu (256, 258) decided that the total volume of chromosomes in wild species with $2n = 14$ was less than in cultivated species. Stolze (755), on the other hand, found no distinct difference in the size of chromosomes in *H. distichum, H. spontaneum* and *H. murinum*. Litardiere (494) observed that the chromosomes of *H. secalinum* ($2n = 28$) had more or less median constrictions like the chromosomes of *H. marinum*, but that they were much smaller.

Tometorp (830) and Ruttle and Nebel (685) observed that there seemed to be only one nucleolus at meiotic prophase and only one pair of chromosomes attached thereto. These observations are in disagreement with some investigators' belief that there is a nucleolus for each satellited chromosome in somatic cells and for each pair of satellited chromosomes at prophase of meiosis. Burnham (118) observed two nucleoli in a few microsporocytes. In some cases a pair of chromosomes appeared to be attached to each. Heitz (351) used *H. vulgare* among a number of species from 13 genera, in his study of the relation of satellites to nucleoli. He concluded that nucleoli develop at telophase on each strand which connects a satellite with the main part of a chromosome. Thus there were always even numbers of nucleoli in diploid, but there could be odd or even numbers in haploid generations of cells. Ghimpu (256) showed two nucleoli in a root-tip cell of *H. bulbosum* ($n = 7$) in which the number of satellited chromosomes had not been determined. However, evidently no particular effort was made to establish the relation between number of nucleoli and satellites in the various other species studied. Moreover, other workers have since shown that Ghimpu was possibly in error in reporting only two satellited chromosomes in some of the species. Wertz (882) found one to three nucleoli in cells of the embryo.

Barley was one of a number of plants used by Heitz (352) in a study of the origin and development of the chromocenter. Behavior of the chromosomes and nucleoli was studied in considerable detail.

Ellenhorn (173) was able to obtain somewhat greater linear differentiation of chromosomes in root tips of *H. vulgare* by immersing the roots in a mixture of water and ice for periods from six to 24 hours. The results were deemed to indicate a difference in the reaction to cold of eu- and heterochromatin. Keeping

young seedlings at 0–2° C. for several hours resulted in a marked shortening of the chromosomes (471, 741) and distinct morphological differentiation (741).

CHROMOSOME STRUCTURE. Ruttle and Nebel (573, 685) used barley, among other plants, as material for determining the number of threads in chromosomes at various stages of mitosis and meiosis. They concluded that during mitosis four strands were visible in each chromosome from anaphase through prophase. At metaphase eight strands became visible. At first meiotic metaphase eight strands were judged to be present in each chromosome because they became visible at anaphase. No further split became visible before metaphase II where the chromosomes were again eight-partite as in ordinary mitoses. Inouye (395) noted evidence of two threads at telophase and prophase in somatic chromosomes. The threads seemed to receive material from the nucleolus during prophase (394, 395). The observations of other workers on the controversial subject of number of threads per chromosome are summarized in a table by Ruttle and Nebel (685).

Gustafsson (281), from studies on root-tip divisions following X-radiation of dormant seeds, found that fragments usually occurred in pairs. From that he concluded that the chromatids were single in the resting or interphase nuclei. Paired fragments, resulting from X-radiation of dormant seeds, have been observed by the writer and co-workers to be more or less the rule rather than the exception. Huskins and co-workers (376) were of the opinion that differentiated cells in the root tips were "normally polyploid or polytene".

CHROMOSOME BEHAVIOR. Chromosome morphology and behavior at mitosis (395) and meiosis (393, 394, 396, 397) have been reported in some detail by Inouye. A number of other workers (72, 569, 770) have also given observations on meiosis in normal plants.

Sakai (686) studied the diurnal frequencies of mitoses in root-tip cells of barley and ten other species. There was a marked increase in frequency shortly after midnight and midday in rice and two *Phaseolus* sp. The tendency toward periodicity was not very marked in barley nor in any of the four other species of cereals studied.

Hybridization

ARTIFICIAL CROSS POLLINATION. If clothes make the man, it is certainly true that progress in arts and sciences is limited or promoted by technology. Genetics itself would not be possible without methods for making crosses.

Apparently the cultivated species are all fully self-fertile, but there have been reports (468, 722) that some of the wild species have low fertility when selfed. Spikes of *H. bulbosum* set few seeds under bag (468, 722), and the same was true of *H. brevisubulatum* under greenhouse conditions (722). On the other hand, *H. jubatum* and *H. murinum* had high self-fertility, and *H. nodosum* had intermediate self-fertility in the greenhouse (722).

Hybridization of cultivated barleys is more difficult than crossing wheat, but is, nevertheless, readily accomplished if reasonable care is taken to limit injury to the flowers. A number of methods have been recommended, but Bonnett (85) felt that best results were obtained in emasculating and pollinating by breaking a hole through the lemma rather than by clipping the tops of the florets off as is customarily done. Pope (632) advocated clipping the florets and using a paper cone to facilitate application of pollen. Rosenquist (680) placed the female and male spikes within the same paper bag, holding them close together with an OK paper clip. Occasional shaking of the bag was recommended. Riddle and Suneson (654) obtained the highest percentage of seed-set by brushing a pollen-shedding spike against the floret-clipped spike of the female—a method described by Pope (623). Leaving a portion of the spike to produce selfed seeds has been recommended as a means of increasing the probability of obtaining well-developed hybrid seeds on the same spike (839). Harlan (315), a man with long and abundant experience in making barley crosses, stuck by the procedure of clipping the florets just above the anthers, covering with a glassine bag and applying with forceps pollen taken from a spike similarly clipped.

Riddle and Suneson observed that about 70% of the florets remain receptive to fertilization for six days after first flowering at Davis, California. There was a rapid drop in the number of seed set to 10% by the tenth day. These observations were made with the aid of a male sterile mutant which eliminated the necessity of

emasculating the female parent. The value of male sterile characters in studies involving much crossing has been emphasized (764, 765). Pope (627) increased the interval between emasculation and pollination during which viable seeds were produced to as much as 42 days by keeping the excised culms of the female parent at 36° F. during storage.

The temperature at pollinating time (at Aberdeen, Idaho) was reported to have little effect on seed set (321). However, high temperatures necessitated earlier emasculations, which resulted in greater injury, reduced seed-set and reduced seed size.

Crosses with wild species of barley are more difficult, in part because most of them have very small anthers. However, many of the attempted specific and generic hybrids have failed to develop after the pollinations were made. The latter difficulty was overcome (102–105, 142) by dissecting out immature embryos and culturing them on nutrient media. As better technics for removing and culturing embryos are developed (430), it is probable that many new hybrids hitherto unobtained will become possible. In many instances it seems likely that hybrids do not develop because the endosperm fails to provide an adequate food supply for the growing embryo.

Attempts to store barley pollen have met with only limited success (79, 627, 687–689). However, Sasaki (689) was able to preserve viable pollen for six days in an atmosphere containing 40% humidity. Storage in 50% humidity retained viability better than storage in 30% but not so well as in 40% humidity.

Artificial germination of barley pollen has met with almost complete failure (315, 627, 688, 689), but it is possible to germinate fresh ripe pollen on stigmas (25, 626, 630).

NATURAL CROSSING. Speaking of natural crossing, Harlan (315) stated, "On occasional years a wave of immorality seems to sweep the barley crop and such matings may amount to possibly two percent of the total".

A considerable number of cases of natural crossing have been reported in the literature (22, 123, 168, 224, 525, 537, 602, 659, 692, 802, 833, 860, Miege and Grillot 1933A), but, according to Harrington (327), Robertson and Deming (671) and Stevenson (754), the proportion of natural crosses is low—less than 0.5%

in most varieties. Natural crossing is more common in naked than in covered varieties (833). One variety showed as much as 21% of natural crosses in one year (671). There seem to be greater differences between varieties than between seasons (327, 671), but bad weather reduces the amount of natural crossing (224). Cool weather prolongs flowering and promotes natural crossing (315, 833). Peitel (602) observed 0.19% of readily distinguishable crosses and was of the opinion that the total percentage was considerably higher. Taylor and Harlan (802) noted that natural crossing occurred more frequently in lateral than in central florets. The importance of natural crossing in the origin of new forms has been emphasized (226, 315, 602, 692, Miege and Grillot 1933A).

Krajevoj (457) found that when a mixture of pollen from four varieties was applied to stigmas, there was a very high proportion (69–94%) of self-fertilization. This is contrary to the findings of Forlani (224) with wheat.

GRAFT HYBRIDS, EMBRYO TRANSPLANTATION, CULTURING GRAINS OR EMBRYOS ON ARTIFICIAL MEDIA. Several reports are available of studies in which graft hybrids or embryo transplants have been made (110, 903, 904, 905, 906). Brown and Morris (110) found that developing embryos could be transplanted from one endosperm to another fairly successfully. Some development was obtained when barley embryos were transplanted to wheat endosperms. It was thought possible that success was mainly limited by mechanical difficulties in obtaining close contact between host and scion tissue because of differences in the sizes of the barley and wheat embryos.

Yamazaki (903–906) was successful in making a series of embryo transplants among common wheat, emmer, barley and rice grains. His method involved the use of a gelatin solution to obtain close union between the embryo scion and the host endosperm. Wheat and rice embryos transplanted to barley endosperms germinated and grew especially well. Embryos of wheat and barley transplanted to rice endosperms did not grow well, particularly those of barley.

Methods for grafting culms at nodes in small grains, as well as transplanting embryos, were reported by Plotnikov (615).

Various media, such as water (110, 111) and nutrient solution-moistened sand with and without sucrose (406), nutrient solutions (110, 111), and starch (110); nutrient media plus casein hydrolysate (432, 433) or tomato juice, etc. (432); have been more or less successfully used for culturing immature embryos.

Cytological Technics

Condensed chromosomes of barley are reasonably favorable for cytological study. Small anthers in some species make for a paucity of material, however. Efforts to analyze barley prophases in the way possible with maize have been made by a number of workers without significant success. The reader is referred to the paper by Smith (733) for details on the use of the acetocarmine smear method on barley, and to papers cited in the section on Histological and Ontogenetic Studies for histological technics.

Sources of Heredity Variations

NATURE. The frequency of spontaneous hereditary changes in barley is by no means negligible. Elsewhere in this paper the spontaneous mutation frequency is discussed, but it might be informative to consider the types of hereditary changes that have been observed in untreated populations. Some idea of the large number and variety of chlorophyll and morphological variants that a group of barley workers observed over a period of years may be obtained by reading the paper by Martini and Harlan (514) and the book by Harlan (315), in which some of the spontaneous mutants are described briefly. Additional indications as to the variety of mutant characters that have been observed in barley may be had by glancing at Table II, which is by no means complete. There is, however, a considerable frequency of irregularities (such as branched spikes, one or more supernumerary spikes produced on necks originating in the last node, twisted necks, abnormal florets, (80, 90, 272, 475, 540, 548, 659, 883) that are usually not genetic in nature (80, 540), although in some cases branched spikes are genetically controlled (90). Miege and Grillot (540) described five types of proliferation in the spike, only one of which (sterile florets in hoods) seemed to be inherited. Some varieties were more prone than others to develop some of the other abnormalities, such as branched spikes and supernumerary spikelets.

Environmentally determined irregularities are so prevalent on occasion as to cause concern (*272*, 883).

Didus (157, 158) observed spontaneous mutants of 22 types during three years of study with two varieties of barley. One of the mutants had awns on the palea as well as on the flowering glume. Another developed a spikelet on the basal bristle of the grain. Other mutations affected genes controlling length of awns, earliness, winter habit of growth, dwarf stature, density of the spike (both more lax and more dense), size of the grains, resistance to *Helminthosporium* and drought, anthocyanin in the leaves, and increases and decreases in yield. A later report on these studies and a similar study on wheat was also published (152).

Pope (625), in a 15-year study of selection for internode length involving the examination of 35,000 plants, found one mutation for internode length, one for irregularly spaced nodes, and suspected that another for a minor change in internode length had occurred. This indicates that though many spontaneous mutations have been observed, the barley genotype is remarkably constant, as was stated by Beaven (53). Kraus (382) found that most variations in pure lines did not persist. Some quantitative differences did continue for two to four generations. It was concluded that selection was much more effective between than within lines.

The importance of spontaneous mutation in the development of new forms has been emphasized (226). Harlan (315) went so far as to state that it was his belief that "a mutation . . . stimulates the production of other variations".

AGE. Age has been reported to produce chromosomal and genic changes in seeds (145), but the writer has been able to find little information on the effects of age on genetic stability in barley. As a result it is not possible to suggest to what extent spontaneous variations may be attributable to aging of the seeds. Since 71% of some types of barley were shown by Robertson and co-workers (674) to be viable after storage for up to 22 years, and Haferkamp (303) found even higher germination in some seeds stored for 28 years, it would seem that barley would provide favorable material for studying the effect of age on chromosomal aberrations and mutation rate. Some contradictory reports on the effects of age

on mutation are reviewed under the section of Mutation Frequencies.

Haferkamp (303) noted that there were chromosomal aberrations (bridges) in ten of 313 root-tip cells from 28-year-old seeds of four varieties of barley, but that there was no similar aberration in 81 cells from root tips of seeds less than a year old.

Todaro (826) reported evidence indicating that barley seeds did not retain their viability so long as did seeds of common wheat and oats. Haferkamp (303), on the other hand, found that seeds of all of nine varieties of barley tested retained a fairly high percentage (up to 100%) of germination for 24–28 years, while only three out of 105 varieties of wheat germinated at all—and those weakly. Seeds of six varieties of oats stored for 27 years also germinated poorly. Preliminary tests with 33-year-old seeds of a number of cereals from an entirely different source have given similar results (W. L. Nelson and M. H. Haferkamp, Unpub.).

HIGH AND LOW TEMPERATURES. Goodspeed (1910A) studied the relation of high temperatures, 56° to 76° C. for two to 70 minutes, to duration of life in seeds, and concluded that the temperature coefficient was reasonably close to expectation on the basis of van't Hoff's Law. Atanasoff and Johnson (1920A) reported that seeds of barley and a number of other cereals survived a treatment of 100° C. for 30 hours. The heat treatment was partially or completely effective in controlling a number of disease organisms. Several earlier papers on the effect of high temperatures on seed-borne diseases were cited by these workers. Neither Goodspeed nor Atanasoff and Johnson analyzed their material for cytological or genetic effects.

Heat is a relatively ineffective agent for producing mutations. However, Peto (611) reported an increase in the mutation frequency for yellow types following a treatment with high temperatures (85° C. for 105 or 115 minutes), but there was no significant increase in the occurrence of white mutants. There was a ratio of one yellow mutant to 13,400 normal seedlings following treatment, and one white to 45,000 normals. No control was tested, but a number of experimental farms and a farmer's field were gone over for an approximation of the spontaneous frequency. Yellow seedlings were found in various ratios from

1 : 500 to 1 : 78,200 normals; whites in ratios from 1 : 4,500 to 1 : 22,500. No yellow plants were observed in four other fields. In the heat-treated material, only four yellow and three white mutants were found, so it is problematical whether the heat treatment was effective in increasing the mutation frequency. Among the plants grown from treated seeds were two with broad yellow stripes, apparently similar to those resulting from irradiation. Gustafsson (297) treated both dry and germinating seeds with heat and found three or four mutants in 473 plant progenies—a 15-fold increase over the frequency in untreated material. Smith and Caldecott (732) found that a barely sublethal heat treatment (75° C. for 30 minutes) produced very few mutations. However, Plough and Ives (616) were able, by means of carefully controlled and extensive experiments with heat treatments, to obtain a six-fold increase in the mutation frequency of *Drosophila*.

Peto (608) found that treatment of dormant seeds of barley at 95° C. for 25 minutes, or at 40° C. for 30 days, resulted in chromosomal aberrations in about 30% of the cells of young seminal roots. The proportion of "mutated" cells diminished to 9% in root tips taken 40 days after heat treatment. The aberrations consisted mainly of fragments. High frequencies of fragments and other aberrations were also obtained by germinating seeds at 35–36° C. (609). Tetraploid cells were among the irregularities observed in root tips from the heat-treated seeds (609, 610).

A temperature of 35° C. for ten hours applied to spikes on excised culms has been reported to result in meiotic irregularities (597). Others have been unable to show that heat treatments on dormant seeds have any distinct effect on chromosomal aberrations (121, 727, 728, 732) or gene mutations (732).

The chief genetic effect imputed to high temperatures has been the induction of chromosome doubling in various species, including barley. Although heat is nowhere nearly so effective in producing autotetraploid cells as colchicine, nevertheless, a number of tetraploid barleys have been produced by temperature treatments, as will be seen in the section on Autotetraploids. Treatments, sometimes in the form of temperature shocks and sometimes as continuous high temperatures, have been applied to young seedlings or to spikes shortly after fertilization.

Smith (727, 728) found no evidence that seeds of autotetraploid

barleys were any more tolerant of high temperatures than were seeds of diploids.

Evidence has been presented to show (121, 727, 728, 732) that heat treatments may modify the effects of X-rays, and, conversely, that X-radiation can modify the effects of heat treatments (121).

It has been noted (471) that low temperatures (2° C.) result in aberrant mitoses, in which the chromosomes go to the poles without dividing. A combination of colchicine and cold treatments administered simultaneously resulted in a greater contraction of the chromosomes in barley than in onion (471).

IRRADIATION—X-RAYS. Some of the earliest experiments that demonstrated the capacity of X-rays to produce heritable variations were performed by Stadler on barley (742, 743). Since that time barley has been one of the favored subjects for testing the biological effects of irradiation. Since X-rays are highly potent and widely available for genetic experimentation, most of the voluminous literature on the subject deals with the effects of X-rays rather than other forms of irradiation. No attempt will be made to review the literature dealing with radiation effects, except insofar as barley was impinged upon. The reader can pursue the subject further by consulting the book by Lea (476) as well as the older volumes of Duggar (163) and the review paper of Goodspeed and Uber (263).

There have been numerous reports that mild doses of X-rays stimulate dormant or germinating seeds of various plants. Both X-radiation and ultra-violet radiation have been reported to stimulate enzyme formation and germination in barley (151, 529). Dittrich et al. (1950A) reported that doses of up to 1,600r of fast electrons stimulated growth. Glutathione seemed to be increased by low doses of X-rays, but decreased by heavier doses (887). Other reports have purported to show that X-radiation does not stimulate seeds. Tascher (791) tested the possibility of X-ray stimulation rather thoroughly with barley and eight other crop plants, concluding that there was no evidence of improved yields resulting from light doses of X-rays. Leopold (484) reported that irradiation resulted in increased tillering, presumably by "opposing or destroying auxin".

Caldecott and Smith (121), and Smith and Caldecott (732)

showed that under certain conditions, X-raying heat-treated seeds resulted in a remarkable recovery from injury caused by high temperatures. Over a considerable range of X-ray doses, seeds that had been " killed " or inactivated by heat were " resuscitated " by subsequent irradiation. Pretreatment with X-rays also prevented killing by a " lethal " heat treatment at certain doses of X-rays. This " protection " was not linearly correlated with dosage; that is, certain heavy and relatively light doses protected the seeds, while intermediate doses provided little or no protection. In these tests seeds given certain doses of irradiation did appear greatly stimulated as compared with seeds given heat treatment only, but not as compared with untreated seeds. Suskind (1950A) did not obtain " resuscitation " of heat-inactivated seeds as reported by Caldecott and Smith (121).

Whether mild doses of X-rays do or do not stimulate the growth of seeds may be debated, but there is no doubt that heavier doses injure seeds (121, 183, 185, 229, 230, 237, 282, 291, 583, 727, 728, 744, 791, 792, 882, Tschechow and Kartaschowa 1934A, and many others). This injury is expressed in more or less pronounced " flecking " on the first leaves, chimeras (731a, 744, 745, et al.), reduced rate of growth, and killing. Tascher (791) noted that the percentage of seeds with coleoptiles but no plumules increased with increasing dosage of X-rays. He also studied the tolerance of dormant seeds of 24 crop plants. The dose (given at 105 Kvp., 4 ma., 500r per min., 22° C.) that killed approximately 50% of the seeds ranged from 4,000r for rye to 85,000r for alsike clover. The corresponding dose for barley was 18,000r. These results are in fairly close agreement with those of Gustafsson (281) who studied the X-ray tolerance of a considerably larger number of crop species.

Freisleben and Lein (230) reported that the percentage of barley seeds that produced harvestable plants in 1941 decreased from 88% in the control to 50% in the lot given 14,000r. In 1942 the percentage decreased from 29% for a lot given 8,000r to 0.14% for a lot given 25,000r. The number of irradiated seeds ranged from 2,000 to 15,000 per dose.

The degree of injury or the amount of radiation required to kill seeds is dependent on a number of factors. Large barley seeds have a greater tolerance than small seeds (237, 297). Increas-

ing the moisture content decreases the tolerance (236, 280, 282, 285, 334, 743, 744, 791, 882, et al.). Tascher (791) showed that the dose required to kill seeds decreased by about half after six hours of soaking, at which time the moisture content was 34% as compared with 10% in unsoaked seeds. The soaked seeds were X-rayed in the steeping water. He also showed that sensitivity to X-ray injury and respiration rate increased markedly during the first 40 hours of aeration after the soaking period. It was observed (791) that a continuous treatment applied to germinating seeds resulted in about the same degree of injury as twice that exposure given in six equal increments at hourly intervals. On the other hand, intermittent treatments on dormant seeds were more injurious than the same total dose given in one exposure.

Wertz (882) considered in some detail the relation of moisture content of seeds to X-ray injury. Measurements were made on the growth of roots, coleoptiles and leaves. In general, injury was directly correlated with the moisture content of the treated seeds. Roots were most reduced in length, coleoptiles the least. The uptake of moisture was slower in a refrigerator at 0–1° C., but when the seeds soaked at this temperature had a moisture content about equal to that of seeds soaked at 22.3° C., the susceptibility to injury was about the same. Light had little effect on the absorption of water or on the X-ray injury. The significance of the results in relation to "sensitive" or "Treffer" volume was discussed at considerable length.

According to Gustafsson (280, 281, 283, 297), X-ray tolerance decreases with increasing age of the seeds. There is also evidence that storing irradiated seeds for a time before planting reduces the survival (297, 744, 791). The storage temperature is also important. Irradiated dormant seeds stored for seven weeks, and irradiated germinating seeds stored for 24 hours at 6° C., 22° C. and 38° C. had much better survival at the lowest storage temperature (791).

Temperature of the seeds during (745, 791) as well as before or after (122, 297, 727, 728, 732, 791) treatment also affects the degree of injury. Dormant seeds treated in solid CO_2 tolerated approximately 1⅔ times the dose tolerated at room temperature

(745, 791). Germinating seeds irradiated at 10° C., 24° C. and 35° C. received the greatest injury from a given dose at 10° C.—the least at 24° C. A heat treatment preceding irradiation has been shown to give seeds a measure of protection from subsequent irradiation (122, 297, 727, 728, 732). Heat applied after irradiation may add to or subtract from the injury resulting from irradiation, depending upon the combinations of treatments applied (122, 727, 728, 732). Tascher (791) showed that the injury to dormant seeds was increased if the seeds were kept at 45° C. instead of at 22° C. during the intervals between intermittent X-ray treatments.

Leaching germinating seeds to remove growth-promoting substances made them more susceptible to X-ray injury (185).

Another factor that affects the degree of injury resulting from irradiation is the atmosphere surrounding the seeds during treatment (334, 728). Irradiating dormant or germinating seeds in a vacuum or in N_2 resulted in a distinct reduction in injury, as compared with the injury resulting from the same dose of X-rays applied while the seeds were in air or O_2 (334, 728). The mutation frequency from seeds irradiated in air was 1.5 times, and the chromatinic bridge frequency was 4.7 times the frequencies induced by the same X-ray treatment applied to seeds which were in a vacuum when irradiated.

Still another factor which affects X-ray injury symptoms is number of chromosomes. Autotetraploid seeds have a considerably greater tolerance than diploid seeds (555, 727, 728).

Fröier and Gustafsson (237) observed that seeds with hulls would tolerate more X-radiation than hull-less seeds. A dose of 25,000r killed 95% of dormant covered seeds containing 14% moisture (236, 237). A dose of 12,000–15,000r had a similar effect on seeds of hull-less types (237). Six-row types were injured more than two-row varieties (291).

Tascher (791, 792) made an interesting test to determine whether seed-borne diseases could be controlled by irradiation. It was found that the dose required to control loose smut of barley also killed about 95% of the germinating seeds. Treatments on dormant seeds were not effective in controlling the fungus. Either irradiation of seeds of various other crop plants was ineffective in

controlling the pathogen without killing the seeds, or the differential between killing doses for the parasites and the seeds was too slight for practical utilization.

In addition to the injury symptoms mentioned above, X-radiation results in certain other effects on the (X_1) plants grown from treated seeds. Some plants have narrow leaves and/or various ear deformities (499). Most of these anomalies are not inherited and the chromosomes behave normally.

Wolcott (895) studied the effects of X-radiation on the anatomy of leaves and stems of barley, as well as a number of other species, and found that irradiated leaves were thicker, shorter and more unsymmetrical than untreated leaves. Irradiation resulted in a proliferation of colorless parenchyma and spongy tissue—as well as an increase in cell size. Some cell walls seemed to lack reinforcement, and vascular tissue was delayed in development.

Irradiation of young seedlings affected the carbohydrate content for at least the next 70 days (411). There was little difference in sugar content between irradiated plants and controls, which was in contrast with results obtained with sunflowers, but it was concluded that treated plants either produced more starch or were unable to translocate it into the seed.

According to Nilova (579), X-radiation reduced the catalase activity of seeds. Amylase activity was reduced in sprouts of irradiated seeds but was not much affected in dry seeds. Activity of proteolytic enzymes was greatest in seeds that were given the X-ray dose that produced the most mutations. Small doses (25r per week for three weeks) of irradiation, applied at certain seasons of the year, resulted in an increase in the number of flower primordia and in the number of tillers (485). This was accounted for on the assumption that the irradiation destroyed some of the auxin in the plants.

So far as is known, the types of mutants and chromosomal changes produced by X-rays are the same and in approximately the same proportions in relation to each other as occur spontaneously. Most induced mutations segregate as simple recessives (731a, 744, 745, et al.). Stadler reported that 95% of the seedling mutants were chlorophyll variants; the remaining 5% consisted of a wide range of morphological types (746). Seedling mutants comprised about 90% of all visible mutations induced (743). On

the other hand, Stubbe and Brandlow (759) reported that the most common of the 34 induced mutants they studied were spike characters.

Pioneer work by Stadler (744, 745) on the relation of wave-length to genetic effects of X-rays showed that equal doses at 40 and 116 Kvp. produced mutations at about equal frequencies. He also obtained mutations with "grenz rays" from a tube operated at seven and ten Kvp. The wave-lengths tested ranged from about two angstroms to 0.009 Å.

Mutants are obtained whether seeds are planted immediately after being irradiated or not (281, 284, 743, 744).

X-radiation of seeds, pollen or eggs also produce various types of chromosomal aberrations (121, 251, 280, 281, 727, 731a, 732, Tschechow and Kartaschowa 1934A). Tschechow and Kartaschowa (1934A) reported observing rod and ring fragments and translocated chromosomes as well as the absence of chromosomes in metaphases of root-tip cells following irradiation of dormant seeds. As many as 60% of the cells had aberrant chromosomes as a result of some of the longer treatments. Frequencies of these aberrations per r unit increase with increased moisture content of the treated seeds (151, 280, 281, 283). Increasing the moisture content of seeds raised or lowered the percentage of disturbed cells with fragments and raised or lowered the percentage with bridges, depending upon total frequencies of aberrations per cell (280). Frequencies of aberrations also increased with age of the treated seeds (280, 281, 283), with lapse of time between irradiating and planting (281, 283), and with increase in chromosome number (727, 728). Gustafsson (289) reported that as high as 70–80% of the mitoses were irregular in root tips of heavily irradiated seeds, although a small proportion of the plants reached maturity.

Fragments observed in root tips grown from X-rayed dormant seeds are usually in apparently identical pairs. From this and observations of effects of irradiation on germinating seeds, Gustafsson (281) concluded that chromosomes in the resting stage are single, unsplit threads and that the "split" occurs near the end of the resting stage. It was believed that higher moisture content was associated with ending the resting stage and division of the threads, thus increasing the frequencies of induced breakages and the proportion of heterogeneous fragments. Gustafsson (280, 281,

283) observed that frequencies of aberrations, and mortality (283) were correlated not only with moisture content but with position in the radicle—the highest frequency of chromosomal aberration and highest moisture content being in the center. This was associated with the fact that divisions occurred first in the center of the root.

The effects of certain substances on the response of chromosomes to X-rays have been tested. Heteroauxin had no appreciable effect on the frequency of chromosomal aberrations (251). On the other hand, Patterson (600, 601) found that neutral red greatly sensitized root tips to X-ray injury. Roots irradiated for one hour in sunlight in a 1:75,000 solution of neutral red, and transferred to distilled water one hour after treatment, were mitosis-free seven hours after treatment. Other roots irradiated simultaneously, but in distilled water, had only a 40% decrease in mitoses. The effect of some additional substances on X-ray-induced changes is discussed under Mutation Frequencies.

Another effect of X-rays on plants grown from treated seeds is chimeral striping of the chlorophyll (229, 731a, 744, 745). Such striped tillers are fairly common, but usually only one or two on a plant are affected. Most of the stripes are either more or less pure white or yellow (green). Peto noted two such striped plants growing from heat-treated seeds (611). They have also been observed following treatment with neutrons (299) and from atomic bomb-induced radiations (731a).

One effect of X-radiation is a reduction in fertility (118, 147, 229, 230, 289, 297, 299, 300, 301, 499, 522, 612). Freisleben and Lein (230) found that in 1941 the average fertility decreased from 88% in the control to 50% in plants grown from seeds given 14,000r. In 1942 the fertility decreased from 54% in plants grown from seeds given 8,000r to 36% in those given 25,000r.

The effect on fertility parallels the frequency of chromosomal aberrations in some cases (251) and, according to Gustafsson and co-workers (284, 292, 297, 300, 301), parallels the "drasticity" of mutations. Gustafsson (284) also obtained evidence that certain types of mutations (e.g., to white) affected larger sectors in the spikes than other types (e.g., to virescent) (284). He believed that mutations to white involved a more minor change in the chromosomes than mutations to other chlorophyll types such as vires-

cent (284, 285). Similar differences were apparent in the types of mutants found in progenies of plants with various degrees of sterility (285, 286, 294, 295, 297, 301, 557). For example, yellow mutants were not found in the progeny of highly fertile X_1 plants. Moreover, certain types of mutants comprised a larger or smaller proportion of the total number of mutations, depending upon the dosage and moisture content of the irradiated seeds (285, 286, 294, 297, 557). It seems to the present writer that "plant" fertility can be only irrelevant with respect to the association between type of mutant and plant sterility, since a mutation ordinarily affects a sector in only one spike, not the whole plant. A general effect on plant fertility might suggest a physiological rather than a genetic modification. Müntzing (557) and Freisleben and Lein (229, 230) also questioned the findings of Gustafsson on the relationship between sterility of X_1 plants and the type of chlorophyll mutant. The latter authors observed (230) a correlation between dosage and fertility of X_1 plants, but not between fertility of X_1 plants and type of chlorophyll mutant.

Gustafsson (283, 284) was also of the opinion that moisture content and storage of irradiated seeds for a few months before planting resulted in an effect on the type of mutants, giving a higher proportion of white "micromutations". Old seeds that were irradiated also had a higher proportion of white mutants (283).

Pismenko (612) treated plants at various stages of development but noted that greater sterility resulted from treatments applied shortly before flowering than from earlier treatments.

Gelin (251) and Gustafsson (285) found a correlation or "parallelism" between the frequencies of chromosomal aberrations in root tips in X_1, cases of sterility in X_1, and mutations discovered in X_2. Gustafsson (285) believed that sterility and mutation frequency were connected phenomena.

Generally mutations, both spontaneous and induced, are deleterious. However, Gustafsson has emphasized the fact that some mutants excel the parent variety in some agronomic character, including yield (286–289, 292, 294, 297, 300, Gustafsson and Nybom 1950A), quality (294, 297, 300), straw strength (294, 300), drought resistance (294), earliness (300) and competitive ability (300). He believed (294, 297, 300) that there was a correlation

between the yields of mutants and the fertility of X_1 plants from which they were derived. Some of the mutants obtained were six-rowed, winter-habit, earlier, later, stiffer-strawed, larger-grained, higher protein content, higher starch content and shorter dormancy types. The winter-habit types were not winter-hardy—supporting the evidence of some (see discussion of Winter-hardiness) that these two characters are controlled by different genes. Spontaneous mutants with 20–25% increases in yield over parent varieties have been reported (158). Others (228, 231, 232) have also emphasized the possibility of agronomically valuable mutations. Freisleben and Lein (232) obtained mildew-resistant lines in X_2 and later generations after irradiating seeds, as well as mutants with increased yield, earliness, etc. Didus (158) found spontaneous mutants with increased resistance to *Helminthosporium*. Honecker (365) related that one of the most important brewing barleys in Germany was a short-strawed mutant form. Thunaeus (817) also reported that some X-ray-induced mutants may have improved brewing qualities. Other mutants, themselves not valuable for cultivation, have been used as sources of germ plasm for improving commercial varieties (703).

X-radiation has been reported to be effective in producing haploids and polyploids in certain genera, not including barley, but its efficacy in these respects is by no means undisputed.

OTHER TYPES OF IRRADIATION. Stadler (742) demonstrated that radium produced an appreciable increase in frequency of mutation in germinating seeds. There was no obvious difference in the types of genetic changes produced by radium and X-rays in these experiments or by other workers on other plants. Since X-radiation has a number of practical advantages over radium for genetic experiments, radium has not been used extensively as a source of radiation.

Exposure to atomic-bomb-induced radiations resulted in effects in every way comparable to exposure to X-rays (731a). The comparisons between the effects of irradiation from the two sources included observations on germination, mottling on the first leaves, chimeras, interchanges in X_1 plants, seedling mutation frequencies, and types of mutants obtained in X_2. The bomb-induced effects were about equivalent to those produced by 16,000r of X-rays.

Neutrons produced effects similar to those of X-rays (299, Thompson et al. 1950A). There was evidence that they produced a higher frequency of chimeras and greater sterility in the treated (N_1) generation, and probably a higher seedling mutation frequency in N_2 than did X-radiation.

Arnason and co-workers (29, 30, 31) reported that radioactive phosphorus (P32) did not produce any detectable chromosomal aberrations in microsporocytes of barley grown in cultures containing minute concentrations of the radioactive material, but several chromosomal aberrations were found in tetraploid and hexaploid wheat grown under similar conditions. The radioactivity from radioactive phosphorus was not noticeably toxic, but that from certain concentrations of radioactive strontium was sufficient to inhibit growth (740). Ehrenberg et al. (166) found that P32 in concentrations of 5–25 micro-curies per seed resulted in a strong inhibition of growth (death at the higher concentrations). P32 caused a high frequency of chromosomal aberrations. Five micro-curies per seed produced disturbances corresponding in frequency to the effects of 10,000r units of X-rays. Most of the aberrations for the first three days after treatment consisted of fragments. The relative proportion of bridges was higher in seeds treated with low concentrations, and with increasing time after treatment. Barley was considerably less susceptible to P32 injury than were *Triticum vulgare* and *T. durum*. This evidently was associated with the fact that these wheat species absorbed more of the P32 than did barley. Apparently, also, the P32 absorbed by the barley was concentrated more in the seed and less in the stems and roots as compared with the wheats. Thompson et al. (1950A) have extended these observations to show that P32 produces a high frequency of seedling mutants. The frequencies per head progeny in one series of treatments were 8%, 4.5% and 3%, respectively, for neutrons, P32 and X-rays.

Treating dry or soaked seeds with ultra-violet radiation stimulated freshly harvested seeds to germinate (422).

Bitter (69, 70) observed no appreciable effect of high radio frequency irradiation (60–180 megacycles per second) on the germination of seeds, nor on the growth of plants obtained therefrom.

It was reported (71, 269) that an electric current of 0.5×10^{-10} ampere stimulated growth if it passed through seedlings with the positive electrode above the coleoptile. A similar current passing

in the opposite direction stimulated elongation of the coleoptile for only about the first hour (71).

CHEMICALS. In general, chemicals have no specific effect on genetic processes. Notable exceptions are the chemicals that affect the spindle, resulting in chromosome doubling. These will be discussed further in the section on Autotetraploids.

As is well known (154, 167, 241, 333, 471), colchicine is especially effective in producing changes (usually doubling) in chromosome number. A considerable number of autotetraploid barleys have been produced with the drug (see section on Autotetraploids). Karpechenko (426) reported observations on some of the cytological effects of colchicine on barley, including transverse division of centromeres.

Shmuck and Gusseva (715) showed that acenaphthene and 11 more or less related compounds were "biologically active" when tested on wheat and barley, but not all of them were as effective with legumes and tobacco. The "activity" was principally expressed in somewhat the same way as that of colchicine.

Gavaudan and Gavaudan (249) observed that apiol produced cytological aberrations, including polyploid cells, in root tips of barley and other plants. Parsley contained a high enough concentration of apiol to produce the irregularities in plants grown nearby.

According to Stebbins and Steinitz (751) and Steinitz (753), keeping germinating seeds in an atmosphere of nitrogen resulted in irregularities in all or almost all of the mitotic divisions in root tips and shoot meristems. Absence of oxygen was considered to be the main cause of the fragments, clumping, anaphase bridges and extrusions of chromatin that were observed. These aberrations were present in material fixed after 12 and up to 144 hours in N_2. Seedlings left in N_2 more than four days did not survive when returned to air. Whether or not the irregularities were transmitted to succeeding generations was not reported. Abnormalities in the spike, etc. induced by 2,4-D sprays were not inherited (8). One of the effects of 2,4-D is to produce abnormalities in spikes similar to those in *H. irregulare*. G. A. Wiebe[3] has shown in several tests that irregular spikes can be produced on

[3] Unpublished observations.

the six-rowed Manchuria variety when 2,4-D spray is applied in the early stages of growth, 20 to 30 days following emergence. The ester form of 2,4-D was used most extensively, but other forms also are effective. The results indicate that 2,4-D duplicates the gene action of certain Abyssinian varieties that normally produce irregular spikes. It is not known by what means 2,4-D brings this result about. The character is non-heritable when artificially produced in Manchuria with 2,4-D, but is heritable in the Abyssinian varieties.

Patterson (600, 601) found that neutral red (1:75,000) had relatively little if any effect on divisions of cells or growth of barley roots.

There is some evidence that mercury compounds in commonly used seed disinfectants, such as Ceresan and Granosan, occasionally cause chromosomal aberrations, including doubling, in some cereal seeds (708). Growth was shown by Euler and co-workers (183, 185, 189) to be inhibited by thiamine, penicillin, digitonin, B vitamins and a number of other organic compounds.

Nitrogen mustard gas produces some sterility in the treated (M_1) generation and an increase in the frequency of seedling mutants in M_2 (299). "The mutation rate after a treatment with a 0.01% solution for 40 minutes corresponds approximately to an effect of 1,200 r-units" (p. 384) of X-rays.

Kiessling (440) found mutant-striped (which also gave rise to white) seedlings in the second generation following injection of plants with a solution, 1:5,000, of KNO_3. Further injections did not produce additional mutants, so it is questionable whether the new mutant type was induced by the chemical treatment.

POLYEMBRYONY. Twin seedlings frequently differ with respect to number of chromosomes. This is apparently true with barley as well as a number of other genera (553). Müntzing (553) found one triploid and two haploids among 93 twin barley plants observed. Observations on the haploids were reported by Tometorp (830). Terao and Ikeda (809), Schulz (707) and Higgins (356) also reported that twin, and even triplet (809), seedlings sometimes grew from seeds of wheat and barley, as well as a number of other crops (356). Pope (631) observed the normal diploid number of chromosomes in two sets of twin embryos.

SELECTION, HYBRIDIZATION AND ENVIRONMENT. Most geneticists are more or less familiar with reports of Russian biologists relating successes in modifying hereditary characters through breeding and selection. Some of these studies have been on barley. Judin (417) reported obtaining naked from covered types after six years of selection. Simultaneously selection for a luxuriant root system was practiced. An abundant root system was associated with vigorous tillering, many and large leaves, uniform ripening, large and white seeds, resistance to disease, and frost resistance. Some of the plants had culms arising from the lower nodes, and branching of ears that resulted in increased seed production.

Solovei (739) reported being able to convert the hereditary nature of barley from spring to winter type in three years. Some F_2 plants of crosses were especially susceptible to modification toward more numerous spikes, perennial habit and naked seeds.

Earlier, Kozlov (452) found that growing hulled varieties at various geographical stations in Russia had little if any effect on the expression of hulledness.

Khodkov (435) explained the appearance of winter- and semi-winter-habit types in crosses of spring varieties by assuming that environmental conditions under which the F_1 plants grew modified the genotype.

Two dwarfish, partially sterile, X-ray-induced mutants were crossed by Krajevoj (455), and more or less normal F_1 plants were obtained. Some sterility (up to 12%) was observed, although productivity equalled that of the parent variety, and some culms surpassed the parent variety in height. No segregation occurred in F_2.

Pissarev et al. (613) were of the opinion that a haploid was obtained as the result of stimulating an egg cell of *Hordeum vulgare distichum* with pollen of *Elymus arenarius*. A number of haploids have been found in various genera as a result of attempted crosses, particularly wide crosses.

Mutation Frequencies

The term "mutation" will be limited to refer to heritable "genic" changes and will not include chromosomal aberrations. However, in practice it is often impossible to distinguish between these two types of changes (231, 746).

A number of investigators have studied the spontaneous mutation frequency and found that 0.5% or less of spikes tested segregate new mutants (334, 731a, 732, 742). Gustafsson (297) found seven out of 11,242 plants were heterozygous for mutants. Peto (611) observed 149 mutant seedlings in about 1,390,000 plants in field plantings. Hallqvist (305) found eight of 6,000, and for Freisleben (226) three out of 600 plants were heterozygous for mutants. Didus (157) noted 0.2% of the seedlings were white in a population of 130,000 plants of *H. distichum*. He also observed a number of physiological and morphological variants. Delaunay and Didus (152) reported that the spontaneous mutation frequency for barley was considerably higher than the 0.14% observed in wheat.

Few observations are available on the relation of age to mutation frequencies in barley. Gustafsson (297) tested the mutation frequency in seeds stored for three years with 15% moisture content and found five of 697 plants were heterozygous for mutations —a "fifteen-fold increase". The writer observed (731a) that the mutation frequency in progenies of plants grown from 19-year-old seeds of Moister barley [4] was not much higher than the frequency in one-year-old seeds of Trebi. Unfortunately a control grown from one-year-old seeds of Moister was not available. The old seeds of Moister were no more (perhaps less) susceptible to mutation as a result of exposure to irradiation from an atomic bomb than were the younger seeds of Trebi. The frequencies were $5.5 \pm 0.41\%$ and $7.4 \pm 0.32\%$, respectively.

Mutation frequencies from X-radiation have usually been determined from treatments of dormant seeds (230, 232, 285, 297, 301, 501, 612, 728, 731a, 732, 743), although soaked or germinating seeds have been used in some experiments (285, 286, 301, 334, 501, 612, 743, 744). Lutkov (501) also determined the mutation frequency (2.9%) from irradiating spikes shortly before flowering in comparison with the frequencies from treating dormant (8.8%) and germinating seeds (5.1%). These frequencies were considered to be about maximum for each of the three stages. Pismenko (612) likewise irradiated dormant seeds, seeds soaked in solutions of heavy metals, and spikes before flowering, but the dosages (500 to 4,000r) were not near the limit of tolerance for the dormant seeds. According to Nilsson-Ehle (584), the muta-

[4] Provided by D. W. Robertson.

tion frequency can be increased about 5,000 times by treatment with X-rays.

Mutation frequency is dependent on a number of factors, particularly dosage (230, 232, 301, 743, 744) and moisture content (285, 743, 744, 745) of the treated seeds. It may be affected by the genotype of the treated line (284). Stadler (742) obtained data indicating that impregnating seeds with salts of heavy metals prior to X-raying increased the mutation frequency. Pismenko (612) also tested the effect of impregnating seeds with some of the same compounds (barium, uranium and lead nitrates) on X-ray-induced changes. The absolute frequency varies from experiment to experiment under the most carefully controlled conditions and from observer to observer. Some of the difference is undoubtedly attributable to differences in apparatus and to differences in the handling and classification of "mutants". However, it may be expected that 10,000r, if administered with sufficient voltage for effective penetration, will result in from 3% to 12% of the spikes segregating seedling mutants in X_2. Gustafsson (297) stated that about twice as many mutants were found by testing the X_3 as were found by testing the X_2. Of the mutants, 85% to 90% are "chlorophyll" mutants; the rest are about equally divided between the "morphological" and "physiological" classes (297). Others (232, 334, 583, 731a, 732, 742, 744) have likewise noted that most of the induced mutants are of the chlorophyll-deficient type. Stubbe and Bandlow (759), however, found both morphological and physiological types of mutants more common than chlorophyll defects.

In an effort to determine the highest obtainable frequency of mutations, Gustafsson (286) gave 505 dormant seeds a very heavy treatment (r unknown), from which only 30 plants survived. In X_2 or X_3, or both, 70% of the 30 plants segregated for chlorophyll, morphological or physiological mutants.

Mutation frequency has been generally considered to be proportional to X-ray dosage applied under a given set of conditions (743, 744). However, Gustafsson (286) obtained 45 chlorophyll mutants with 5,000r and only 58 with 10,000r. Expected numbers on the basis of direct proportionality were calculated to be 36.5 and 66.5. Later (301) additional evidence was interpreted as showing that mutation frequency per r-unit decreased with in-

creased dosages. Freisleben and Lein (230, 232) also reported that at higher dosages of X-rays the relative and even absolute frequencies of mutations fell off.

There is considerable evidence that the mutation frequency for a given dose of X-rays increases with moisture content of the treated seeds (283, 285, 743, 744, 746), but there is some evidence that it does not (284). According to Stadler (743, 744, 746), the mutation frequency in germinating seeds was six to eight times as high per r-unit as in dormant seeds. Gustafsson (285) found that with 5,000r the mutation frequency from germinating seeds was 1.5 times, and at 10,000r, four times the frequency from dormant seeds. Stadler (744) reported that merely increasing the moisture content of seeds did not increase the mutation frequency. Soaking seeds in water had to be succeeded by a period of "aeration" before raying for the mutation frequency to be affected. Although the mutation frequency per r-unit is higher in germinating seeds, dormant seeds will survive a dose 15 to 20 times greater than can be survived by germinating seeds, and it is possible to obtain a total mutation frequency about double that obtainable from irradiating germinating seeds.

Observations as to whether temperature of seeds before, during or after raying has any effect on mutation frequency are somewhat at variance. Stadler (743, 744) reported that treating dormant and germinating seeds at 10°, 20°, 30°, 40° and 50° C. showed no significant effect of temperature on the frequency of mutation per r-unit. Dormant seeds packed in solid CO_2 (ca. $-80°$ C.) were able to tolerate a treatment two-thirds heavier than seeds irradiated at room temperature; and the mutation frequency was only slightly if at all lower per r-unit than in seeds treated at about 20° C. (745). Furthermore he found that mutation frequency was unaffected by keeping dormant seeds at a temperature of from $-80°$ to $+38°$ C., and germinating seeds at a temperature of $+7°$ to $+37°$ C. for 24 hours after treatment. Although Gustafsson (297) treated seeds for an unspecified period at 80° C. before raying them and obtained a 50% reduction in mutation frequency, the difference was attributed to desiccation of the seeds. However, Smith and Caldecott (732) found that pretreatment at 80° C. for 30 minutes increased the mutation frequency from 5.8% to 6.9%, based on 1,591 and 2,103 head progenies, respec-

tively. The same heat treatment applied immediately after X-raying increased the frequency to 9.1% in 2,363 head progenies. These data were obtained from only one experiment, but the differences between the highest frequency (9.1%) and the other two (5.8% and 6.9%) were statistically significant.

Gelin (251) found a clear parallelism between frequencies of root-tip cells in X_1 showing cytological aberrations, degree of sterility in X_1 and mutation frequency in X_2. A similar correlation between sterility in X_1 and mutation frequency in X_2 was reported by Gustafsson (285) and Müntzing (557).

Gustafsson (284) and Hallqvist (304, 305) noted that white mutants segregated in more nearly 3:1 ratios from heterozygous plants than did yellow or virescent types. These were spontaneous mutants, but similar results were obtained with 25 X-ray-induced mutations (284). The aberrant ratios were presumed to be caused by elimination of male gametes, resulting almost invariably in a deficiency of recessives. Freisleben and Lein (232) noted that morphological and physiological (field) mutations affected fewer plants in a progeny test than did chlorophyll mutants.

D'Amato and Gustafsson (147) tested the effect of colchicine, KCN, uranyl nitrate, H_2O_2, butter-yellow, $Fe_2(SO_4)_3$, pH and water on the seedling mutation frequency resulting from a given dose of X-rays applied to seeds, and concluded that almost all the pretreatments increased the frequency. They also concluded that pretreatment with colchicine was effective in changing the proportions of the types of mutants, i.e., increased the xantha and rare types. This conclusion was considered to be confirmed by a later experiment (301).

HISTOLOGICAL, ANATOMICAL, MORPHOLOGICAL, ANALYTIC AND ONTOGENETIC STUDIES

No effort is made here to review thoroughly the literature in this field. However, it seems desirable to include a brief section and to assemble some references, so that interested readers will have citations to literature on the subject.

Lerner and Holzer (486), in the 19th century, prepared one of the most detailed and complete publications on the histology and ontogeny of barley yet available. The work included 51 plates

comprised of about 270 finely detailed, drawn figures, particularly of the spike and its components[5]. They also cited a great many earlier publications dealing with barley. Another important detailed study of barley grain and of the histological changes occurring during germination was also made in the last century by Brown and Morris (110). The endosperm was considered to be dead stored material on which the embryo acted as a parasite. Diastase was proved to be secreted only by the "absorptive epithelium" of the embryo. Experiments on transplantation and growth of embryos on foreign endosperms and culture media were also reported.

Arber and co-workers published a number of papers dealing with the morphology and histology of barley and other cereals. Much of the material in these publications was prepared as a book, The Gramineae (28). In this book are over 40 pages of references. Arber (27) also compared the anatomy and morphology of inflorescences of a number of wild and cultivated species of barley in serial sections. Belk (54) made a rather extensive study of the structures of the infloresence of cereals, including some wild species of barley (*H. jubatum, H. pusillum* and *H. murinum*). Bonnett (83, 84), Mostovoj (1931A), Brenchley (1920A) and Noguchi (586) studied the development of the barley spike, primordia of which may be identified as early as 10–12 days after the seed is planted (88, 646).

Viedeman (858) made an interesting histological study of the anatomical basis for fertility and sterility of lateral florets. It was concluded that the lateral florets of two-rowed barleys had complete flowers, but that long thin pedicels resulted in restricted development of these florets—the longer and thinner the pedicel, the poorer the floret.

Melnikov (524) made a histological study of hulled and naked barleys, and concluded that there was an unbroken series of intermediate forms. In some " half-naked " varieties and in some hulled by hull-less hybrids, the palea was attached to the grain, but the lemma was free. The significant difference between hulled and

[5] There is apparently only one copy of this work in the United States. The writer is indebted to G. A. Wiebe for an opportunity to see it.

naked forms was the amount of mechanical tissue in the flowering palea. According to Harlan (313, 315), in hulled forms a sticky substance is secreted from the kernel nine or ten days after pollination (at Aberdeen, Idaho) and causes the glumes to adhere to the caryopsis.

Mostovoj (550) compared the development of florets on hooded and non-hooded varieties, and came to the conclusion that early development was similar. Later the beginnings of awns were apparent on hooded types, but rudiments of flowers began to develop on the awns. These rudimentary flowers were considered to be the cause for the development of hoods.

A detailed study of cell sizes and other quantitative measurements were made by Kaiser (419) on leaves, glumes and awns of barley and oats. Swenson (770) compared the rate of mitosis and growth as well as sizes of cells and organs in normal and mutant (brachytic) barley, and found that the difference in height was attributable to a difference in the number of cells.

A note on the histology of barley roots was published by Bryant (112). An excellent photomicrograph was included. This same author (113) also studied the effect of aeration on barley roots growing in culture solutions. Aeration increased the number and length of roots, thickness of cell walls, and sugar content. Other, more complete studies on the anatomy of roots were reported by Jackson (402) and Wagner (869). Heimsch (347) studied the development of vascular tissue in roots and emphasized the differences in the process, even between roots of the same plant. Kokkonen (443) published extensive studies on the root system of barley and other cereals. Roots were distinguished as to form, structure and function. Observations were also made on changes during the growing period and on the effect of rate of seeding. The primary roots of all varieties tested were observed to grow vertically into the ground, but the angle made by the lateral roots varied with variety (785). Differences between varieties were correlated with geographical latitude. Bystrikov (1931A) also made a rather detailed study of the development and distribution in the soil of the root systems of barley and a number of other crop plants. Harlan (315) distinguished "long, white, shiny roots of large diameter" which he termed "winter roots". Ob-

servations on the ability of barley and other grass seedlings to regenerate roots and shoots after being cut at different places were reported by La Rue (474).

Winfield (894) likewise studied regeneration in decapitated coleoptiles. Milthorpe and Robertson (542) considered that barley roots were essentially similar to those of carrots and beets in their ability to accumulate ions of KCL and KCN.

Erdtman (181), in a study on the pollen of barley and other cereals, found that the pollen grains of barley were comparatively small (about 45 by 43.5 microns), with one small round pore about four microns in diameter. There was no distinct difference between the pollen of two- and six-rowed varieties. Jones and Newell (416) found the diameter of pollen grains of *H. pusillum* to be about 39 microns, and those of *H. jubatum* to be about 43 microns. Hirayoshi (358) observed that the anthers of *H. murinum* (tetraploid) were about 1.6 mm. long, while those of *H. spontaneum* (diploid) were 3.9 mm. long. In shedding, the anthers of the former split about 48%, while those of the latter split only 21% of their length.

Studies on fertilization and development of seeds have been rather extensive. Pope (634) observed that the presence of one pollen tube in the stigma seemed to inhibit the growth of another tube in the same region. No more than one pair of male nuclei was found in an embryo sac, although several might have been near the micropyle. He (630, 632) found that male nuclei were present in the egg sac 20 minutes after pollination if the plants were at a temperature of 30–35° C. (apparently near the optimum). At 5° C. 140 minutes were necessary to reach a similar stage. At 40° and 45° C. no endosperm divisions were observed. Persidsky (606) studied pollination, fertilization and the development of endosperm and embryo from the time of fertilization to germination of the mature seed. Fertilization occurred about six hours, and the first division in the fertilized egg 16–18 hours after pollination. Katterman (430) observed that fertilization occurred about three hours after pollination. Studies were also made on the early stages in embryo-sac development.

Brenchley (94) studied some of the chemical as well as the histological changes in developing seeds.

The reader is referred to papers by Arber (28), Harlan (313), Harlan and Pope (324), Jakovlev (403), Krauss (460), Merry (528), Pope (626, 630, 633) and others (14, 94, 138, 513, 810, 816, 865) for additional information and references to studies on the morphology and development of barley seeds, and to the paper by McCall (520) for a detailed study on the related genus, wheat. Among the studies on development of barley seeds, those of Merry (528) and Krauss (459) are particularly complete.

A number of reports show that viable seeds will develop on culms removed from the plant shortly before (431, 624, 629, 630, 632) or after (79, 323, 325) pollination. Excised culms with their bases kept in water produced a higher proportion of germinable seeds than culms left without water. Gill (259) was unable to obtain viable seeds from plants of *H. nodosum* that were cut off at flowering and allowed to dry in the sun, but viable seeds were obtained from plants of this species when the stigmas had withered and the seeds were "milk ripe".

Going in the other direction, immature seeds have been induced to continue to grow viviparously in the spike (628, 632, 635, 636) or on culture media (105) before maturing.

The respiratory quotient of dormant seeds is about 0.6, while the R.Q. of germinating seeds first rises considerably above 1.0 and then falls to about 0.9 (406). Some observations on the metabolic changes occurring in dormant and germinating seeds (and additional references) may be found by consulting James (405) and James and James (406). Brown and Worley (108) reported that the Q_{10} for the absorption of water by dormant seeds was high—approaching van't Hoff's Law.

Kopecky (447) developed methods for determining the weight, moisture, nitrogen and ash contents of individual grains. The nitrogen and ash contents of single grains were about the same as the values found by macrometric methods for composite ground samples. However, such samples had less moisture than did individual kernels. By these methods it was found that the heaviest grains were in the lower portion of the spike (448, 449). The topmost grains were usually smallest. The moisture content of maturing seeds decreased, but the nitrogen content remained relatively constant.

Wertz (882) reported that at 22.5° C. the first cells to divide in germinating seeds were in the root primordia—at about 18 hours after soaking started. Cells of the leaf and coleoptile began to divide about six hours later.

Germinating barley seeds have an average of about 4.5 secondary rootlets (871). The plumule of some naked varieties emerges near the apex of the seed, while in others it emerges from the same end as the radicle (234). The genetic nature of the difference was not determined.

Pope (618) concluded that the growth curve of barley culms was essentially sigmoid, with minor variations resulting from "the accessibility of nutrients and the structural ability of the plant to translocate them and utilize them in growth".

Observations on the changes in chemical composition of barley plants from the seedling stage to maturity were reported by Norman (587). Engledow and Wadham (179) made weekly observations on dry weight, nitrogen and ash content of developing plants. Gregory and Richards (273) made similar observations and determined the effect of N, P and K deficiencies on respiration and growth. Hubbard and Harper (371) reported that the content of N, P and Ca varied with stage of development and from season to season. Differences in the development of summer and winter varieties, and the relation of the differences to temperature were studied by Almedia (17). Gregory (268) studied the effect of day and night temperatures, sunlight and the evaporating power of the air on the development of barley plants. A study of the variations in chlorophyll and carotin content in leaves of barley, rice and wheat during development was made by Nagasima (567). Catalase activity was found by Pope (620) to vary during the development of the plant, with maxima at three stages—early germination, formation of crown roots, and early jointing. In individual leaves catalase activity was low in young leaves, increased as they matured, and then declined as the tissue died (622).

Walster (870) concluded that high growing temperatures (20° C.) plus high nitrogen supply gave excessive vegetative growth and little culm formation. On the other hand, low growing temperatures (15° C.) and high nitrogen supply gave normal vegeta-

tive growth and normal culm formation. A similar conclusion was reached by Shands (710) as to the optimum temperature for maximum yield.

It has been reported (851) that the protein and nitrogen-free extract in seeds affects the number of culms and yield of plants grown from them.

INTERSPECIFIC HYBRIDS

Compared with the multitude of interspecific hybrids in *Triticum* that have been reported, relatively few wide interspecific hybrids in *Hordeum* have been studied. However, crosses among the cultivated species have been made by so many workers that a listing of them would be a chore.

CROSSES BETWEEN CULTIVATED SPECIES. Hybrids between cultivated species have apparently been almost completely fertile, even though the parents came from widely separated regions (525), and without evident meiotic irregularities. Occasional instances of sterility in F_1 or later generations have been reported, however. For example, Vavilov (855) found a high proportion of partially and completely sterile plants in the F_2 of a cross between an Abyssinian and a Japanese barley.

CROSSES BETWEEN CULTIVATED SPECIES AND SEVEN-CHROMOSOME WILD SPECIES. Crosses involving cultivated species and the wild species, *H. spontaneum* (68, 525, 781, 833, 842, Covas 1950aA, and a number of other workers) have shown no marked sterility or abnormal segregation. Most of the characters of *H. spontaneum* are dominant over corresponding characters of cultivated barleys—with the exception of hoods. Similar results were observed for the cross of *H. vulgare* with *H. agriocrithon* (410). This cross gave regular ratios in both F_2 and backcross populations. Thus it would appear that all of the species in the section Cereale are closely enough related to give fertile F_1's and regular Mendelian ratios.

A cross between *H. vulgare* and *H. muranium* (*murinum?*) was successfully made (512), but the hybrids died in the seedling stage.

CROSSES BETWEEN SEVEN-CHROMOSOME CULTIVATED SPECIES AND 14-CHROMOSOME WILD SPECIES. Quincke (643) obtained hybrids

by pollinating *H. jubatum* × *H. vulgare hexastichum* and × *H. vulgare distichum*. In the first cross only 10% of the seeds germinated, although 70% of the florets set seed. About 54% of the seeds from the second cross grew vigorously and produced plants twice as tall as the female parent. Russian workers (866) crossed the same species, obtaining 101 seeds from 350 pollinated florets. Only two plants grew from these seeds, and they shed no viable pollen. When pollen from cultivated barley was applied to 383 florets, two of them set seed. Attempts to make the reciprocal cross, *H. vulgare* × *H. jubatum*, failed (866).

The cross, *H. sativum* × *H. bulbosum*, was attempted on a large scale by Kuckuck (467, 468). About 10% seed-set was obtained, but the seeds were shriveled and, except for one produced on a two-row winter barley, were inviable. The F_1 plant resembled *H. bulbosum* but had much smaller spikes. Root-tip cells had 21 chromosomes. The plant was sterile, and attempted backcrosses on the hybrid failed. The reciprocal hybrid was made by Vinogradova (866), but the hybrid plant was weak and died early in development.

Some efforts to cross *H. vulgare* and *H. nodosum* have failed (512), but two attempts succeeded. Pollinating *H. nodosum* × *H. vulgare distichum* resulted in 43% seed-set, of which 28% were viable (643). The F_1 plants were vigorous compared with the female parent. Pollinating *H. vulgare* with pollen from *H. nodosum* failed to produce seed (866), but the reciprocal cross resulted in 71 seeds in 303 florets. Of these seeds, five produced plants. The plants had defective anthers but, when pollinated with pollen from *H. vulgare*, set a few seeds.

Matsumura[6] obtained some "poor, shriveled seeds" of *H. sativum* and *H. spontaneum* pollinated by *H. murinum*. The seeds germinated but died in the seedling stage.

OTHER INTERSPECIFIC CROSSES. Smith (721) attempted to cross *H. vulgare* (female) with *H. brevisubulatum*, *H. bulbosum*, *H. jubatum* and *H. nodosum* (males). No seed was obtained, but, particularly when pollen of *H. bulbosum* was used, enlargement of the ovaries was noted. Menabde's attempts (525) to cross cultivated barleys of Georgia with *H. bulbosum*, *H. crinitum* and *H.*

[6] Personal correspondence.

murinum also failed. Chromosome numbers of the plants used in these crosses were not reported. Tschermak (835) stated that crosses between cultivated barleys and *H. murinum* and *H. bulbosum* never succeeded.

Covas (1950bA) observed two univalents in almost 30% of the cells at first meiotic metaphase in the cross of *H. compressum* × *H. stenostachys*. Other irregularities were also common. Only about 16% of the pollen appeared normal as compared with about 95% in the two parents.

INTERGENERIC HYBRIDS

Hybrids between wheat and barley have been reported (264). Two Australian varieties of common wheat, Bobs and Canberra, were reputed to have been developed by Wm. Farrer as a result of crosses between wheat and barley (264). Gordon and Raw (264) attempted to cross Bobs with a two-rowed barley and obtained seeds that produced Bobs-like F_1 plants. In F_2 there was segregation for certain wheat characters, but no barley types appeared in F_2 to F_4. Later, reciprocal matings with a number of varieties of wheat and barley were attempted with somewhat similar results. In no case did a character from the male parent appear in the F_1 or later generations. In only one case was there any evidence of sterility, and this case was attributed to thrips. Cytological observations on F_2 plants revealed that most of them had 42 chromosomes (21 bivalents), but irregularities were observed. In response to an inquiry from the writer for further information on these wheat-barley crosses, Dr. Raw [7] confirmed the earlier report, adding that a "relatively high" mutation rate had been observed in the segregating generations. A B-type speltoid was recognized as one of the off-types. His interpretation of the results was that a "pseudo-fertilization of the wheat ovule had resulted in a parthenogenetic stimulation, accompanied by a doubling of the maternal chromosomes".

Limited attempts to cross various species of wheat with autotetraploid barley were unsuccessful (423).

Efforts to cross *H. brevisubulatum* with *Triticum durum* failed (720, 721).

Reports of attempts to cross cultivated barley with rye are rare,

[7] Letter dated July 22, 1948.

but undoubtedly there have been many attempts that failed to appear in print. In the cross, *H. vulgare hexastichum* × *Secale cereale*, fertilization evidently took place, but development soon ceased, and no viable seeds were obtained (643). Thompson (814, 815) and Thompson and Johnston (816) studied the cross cytologically and found that fertilization took place in 90% of the ovaries. Early development of the embryo was normal, but the endosperm nuclei were very large, few in number, and were not separated by cell walls. After four days the embryos died, and began to disintegrate a few days later. Cessation of development of the hybrid seed was not considered to be caused by the antipodals (103, 142) but by abnormal development of the endosperm. Brink and Cooper (104) reported briefly on observations made on *H. vulgare* × *S. cereale* crosses and found results similar to those they had reported for *H. jubatum* by *S. cereale*—less than normal stimulation of the antipodals. Thus there is no agreement as to what causes the cross to fail.

A cross between *H. jubatum* and *S. cereale* (102–105, 142) has been reported in some detail. Of considerable interest is the fact that the cross was unsuccessful until nine- to 12-day-old hybrid embryos were dissected out and grown on nutrient media (105). Evidence indicated that mitotic irregularities in the endosperm, resulting in the bar to hybridization, was caused by a lack of sufficient nutritive material for the embryo (103, 142). The mitotic irregularities were considered to be the result of malfunctioning of the antipodals. This cross had been attempted before (643), but only shrunken inviable seeds were obtained.

The *Hordeum-Secale* hybrid was much like other wide hybrids at meiosis. Certainly the apparent homology of the chromosomes, as indicated by pairing at microsporogenesis, was as great as homologies of chromosomes in some other generic hybrids (e.g., *Triticum-Aegilops*) that are obtained with ease by usual crossing technics. At diakinesis there were frequently five bivalents and 11 univalents, and at other stages there were associated abnormalities in the form of lagging chromosomes, splitting univalents, bridges, micronuclei, etc., as usually observed in wide hybrids and desynaptic mutants.

Smith (720, 721) was unsuccessful in efforts to cross *H. bulbosum* and *Secale cereale*.

Several efforts to hybridize *Hordeum* and *Elymus* have been reported (46, 47, 720, 752, 833, 835). Smith (720) tried unsuccessfully to cross *H. vulgare* with nine species of *Elymus*. Reznicuk (652) also reported failing to obtain hybrid plants, but others' attempts were successful (46, 47). *H. nutans* and *H. vulgare* were pollinated with pollen from *E. arenarius* and *E. giganteus*. One hybrid on each species was obtained as a result of pollination with *E. giganteus*. The hybrid with *nutans* became vigorous and possessed many characteristics of the paternal parent —coarse foliage and stems, and growth habit—and had 21 somatic chromosomes, which was the sum of the haploid numbers of the two parents. The hybrid with *vulgare* was intermediate in vegetative characteristics and also had 21 chromosomes. Korablin (450) obtained 107 seeds of the cross *Hordeum* × *Elymus*, and suggested that the hybrids might prove useful as a hardy crop. Another attempt to cross cultivated barley with *Elymus* resulted in the formation of a maternal haploid (613).

Smith (720, 721) made extensive attempts to cross *Hordeum vulgare* with five species of *Agropyron*, two species of *Bromus*, *Festuca idahoensis* and *Secale montanum*—all without success.

Stebbins et al. (752) obtained a hybrid between *H. nodosum* (female) ($n = 14$) and *Elymus glaucus* (male) ($n = 14$). The hybrid was intermediate between the parents in vegetative and floral characters, but was quite vigorous. Meiosis was highly irregular, with an average of 17 univalents, four bivalents, 0.6 trivalents, and 0.02 quadrivalents. The hybrid seemed identical in taxonomic characteristics with certain collections of *E. aristatus* Merr., a pollen- and seed-sterile form.

A naturally occurring hybrid between *Agropyron pauciflorum* and *H. nodosum* was studied by Stebbins et al. (752). Artificial crosses between the species, involving a small number of florets, failed to produce a viable seed. The natural hybrids exhibited some of the characters of both parents, being in general intermediate. The plants were pollen- and seed-sterile. Meiosis was highly irregular, with an average of 16 univalents, six bivalents and 0.3 trivalents. No quadrivalent was observed in 53 cells studied. The hybrids were compared with taxonomic specimens of *Elymus Macounii* Vasey and were found to be similar to certain of these specimens which were also completely sterile. Nevski (575) reported having observed naturally-occurring sterile hy-

brids between *Agropyrum oschense* Roshev. and *H. turkestanicum* Nevski (p. 619), and *A. macroura* Turcz. (p. 721). Nevski had, however, placed the two species of *Agropyrum* in the genus *Roegneria*.

Generic hybrids, naturally-occurring and artificially produced, between *H. nodosum* ($n = 14$) and *Sitanion jubatum* ($n = 14$) have been studied by Weibe and Smith (890). These hybrid plants are rather common where the two species normally occur together and are characterized by a highly irregular meiosis and a peculiar behavior of the chromosomes in immature pollen grains. This peculiar behavior is somewhat like a second or "pseudo-meiosis".

EUPLOID CHROMOSOME VARIATIONS

HAPLOIDS. Relatively few haploids have been reported in barley compared with the large numbers that have been found in certain of the other cereals, particularly maize and diploid and hexaploid wheat. This is presumably associated with differences in the development of the embryo and endosperm in barley as compared with these other species.

Tometorp (830) reported two haploids in *H. distichum* which were studied morphologically and cytologically. The haploid plants were found as haploid-diploid twin seedlings. The haploids were shorter, had smaller leaves and stomates. The pollen was almost completely sterile, and no seeds were obtained on a few spikes. Two of the seven haploid chromosomes had satellites. There were usually seven univalents at metaphase of meiosis, but in 5.6% of the pollen mother cells, one bivalent was observed. The second division was highly irregular; and, at the first division in the microspores, some nuclei had 13 or 14 chromosomes.

Haploids have also been reported in *H. vulgare* (397, 409, 553, 613). Johansen (409), in a study of root tips from seeds of a commercial sample of barley, found that about 10% of them were haploids, but before the discovery was made the seedlings had been discarded. Inouye (397) reported that behavior at meiosis in haploids of *H. vulgare* was similar to that described by Tometorp in *H. distichum*.

TRIPLOIDS. Reports of triploids in barley are rare. Attempts to obtain them by crossing diploids with autotetraploids have failed, but two triploids were found as members of twin seedlings (553).

The triploids were not described except to indicate that they were detected because they appeared different from the other members of twins.

A hypo-triploid with $2n = 20$ chromosomes was recently reported by Tsuchiya (1949A). It was obtained by pollinating a tetraploid with pollen from a diploid. The plant was slow and lacking in vigor. Meiosis was irregular in the manner typical of triploids in other species. Univalents, trivalents, lagging chromosomes and micronuclei were common. Pollen fertility was low, but two seeds were obtained on uncovered spikes, perhaps from natural crossing. Application of pollen from diploid plants produced a 46% set of good seeds.

AUTOTETRAPLOIDS. Randolph (644, 645) did an excellent job of summarizing information on desirable and undesirable effects of induced polyploidy in various species of plants. Müntzing (552) had previously published a detailed study of a large number of naturally occurring spontaneous and induced polyploid races of plants. This paper was published before autotetraploid barleys had been available for study, but to a large extent Müntzing's conclusions with regard to autotetraploids in other genera have since been shown to apply to autotetraploid barleys.

Literature on autotetraploids in barley is rather abundant. Several tetraploid races occurred spontaneously (161, 315, 725). A number of others resulted from heat treatments (227, 423, 424, 559, 561, 609, 610, 679). Doubling was induced by heat applied to germinating seeds (609, 610) and from heating spikes shortly after fertilization (424, 561). Müntzing et al. (561) found that keeping the spike for about 30 minutes at 45° C. 18 hours after pollinating was an effective treatment for inducing chromosome doubling. Karpechenko (424) kept pollinated plants at 25° C. for 24 hours; he then subjected them to a temperature of 50° C. for 30, 45 or 60 minutes, and obtained tetraploids. Varieties differed in their susceptibility to chromosome doubling. Pope (632) surmised that 14 to 18 hours at 75° F. would be about the proper time after pollination for applying a treatment to induce polyploidy.

Müntzing and Runquist (560) at first failed to obtain autotetraploids in barley or any other cereal, though success was obtained in other plants; but a number of autotetraploids have since been

obtained with colchicine (124, 161, 274, 425, 559, 591, 592, 718, 772, 879).

Several other chemicals have also been used in attempts to induce chromosome doubling. Acenapthene vapours resulted in $4n$ and $8n$ cells in root tips of barley (250). Quinoline compounds also effected chromosome doubling (719). Favorsky (219) noted that three of 12 chemicals tested induced doubling of chromosomes in root-tip cells. Aurantia, diphenylamine and tribromaniline produced effects indistinguishable from those of colchicine and acenaphthene. The three chemicals were ineffective in inducing doubling in stem apexes. Other chemicals (lupinin, lupinidin, auramin) have also been tested (879).

Doubling the number of chromosomes of barley produces various morphological changes in the resulting plants. Usually the tetraploids are more resistant to lodging (559) with shorter, thicker culms (21, 124, 227, 423, 424, 425, 487, 592), producing a higher yield of straw (274). The leaves of tetraploids are longer (227), broader and thicker (423, 425), with larger (227), more widely dispersed stomates (169, 227, 274), resulting in a higher transpiration rate (169). Exodermal cells are also larger (274). The color has been reported to be darker green in some cases (124, 125, 425), possibly because of larger chloroplasts (227). Spikes are usually more lax (425, 590) and larger (423, 590, 592) although the number of florets on diploid and autotetraploid spikes may be about the same (424, 592), or the tetraploid may have more (592) or fewer florets (227, 423, 425, 592). Pollen grains of autotetraploids are larger than those of the parent diploids (161, 227, 274, 423, 718), but a higher percentage of the microspores is abnormal (227, 679). The number of seeds per spike is lower in tetraploids, partly because of sterility (124, 227, 423, 559, 590–592, 679, 725) that varies with the race of tetraploid (424, 425, 556, 558, 559, 590–592, 679) and with environment. Seeds produced on tetraploid plants are usually larger (124, 227, 423–425, 556, 558, 590, 592, 718), with coarser hulls (423). Some of the seeds are underdeveloped (423), and a lower percentage of them germinates (274, 556). Doubling the chromosome number does not appreciably affect the number of seminal roots (633).

Ono (592) compared nine two-rowed and nine six-rowed tetraploid lines with their corresponding diploid counterparts. There

was little difference between the deviations of the two-row and six-row 4*n* plants from 2*n* plants. The average stem length of the 18 4*n* lines was about 85% of that of 2*n* plants. Other comparisons involved ear length (116%), florets per ear (93%) and kernel weight (138%). The two-row 4*n* lines averaged 73% and the six-row 4*n* lines averaged 67% of the fertility of the 2*n* lines. Similar observations on fertility for the years 1944 through 1948 were presented in more detail (594). There were marked differences between years.

A peculiar difference between diploid and tetraploid Everest was observed by Harland Stevens (reported by Harlan, 315). The seeds of the tetraploid were largely covered, whereas the diploid was naked.

Chin (129) concluded that there was no association between number of chromosomes and size of pollen grains, or cells, or number of stomates among the species of *Hordeum*. Stählin (747) also found no clear difference between cell sizes in species with 14 and 28 somatic chromosomes. However, Andres (23) reported that the diameter of microspores of *H. murinum* was about 1.4 times the diameter of microspores of two wild diploid species, *H. chilense* and *H. pusillum*. Kagawa (418) gave the relative sizes of pollen grains of *H. distichon* ($n=7$) and *H. jubatum* ($n=14$) as 100:62. Griffee (277) found that pollen grains of *H. distichon* ($n=7$) averaged 43.4 mu; of *H. jubatum* ($n=14$), 41.4 mu; and of *H. nodosum* ($n=21$), 50.7 mu.

Tetraploids also differ in varying degrees from parental diploids in chemical composition. Autotetraploid plants have a lower dry matter (169, 274, 487) and higher ash (125, 169, 274) content. Levan (487) noted that leaves on tetraploids had 76% as much green matter and 105% as much water as diploid leaves. There is some evidence that the sugar (sucrose) (125, 169), protein (125, 556, 559) and lipoid substance (125) content are higher in tetraploids. Ekdahl (169) found a higher sucrose content in 21-day-old tetraploid plants, but no difference in hexose content. Greis (274) and Ekdahl (169) reported a lower total N content in tetraploids. Ekdahl (169) also found a 9–21% greater K, 2–19% greater P, and 5–29% smaller Ca content in leaves of tetraploid, as compared with leaves of diploid Opal. A higher nitrate nitrogen content was also present in leaves but not in roots

of tetraploids. The protein nitrogen was 9% less in leaves and 1% less in roots of tetraploids.

Autotetraploidy in barley also results in a number of physiological changes. Tetraploid seeds are slower in germinating (124, 227, 274) than seeds of corresponding diploids. This may be accounted for by a lower respiration rate in the tetraploids (125, 169), although others (21) have found little difference in the respiration rate of diploids and autotetraploids. However, malt diastase activity in germinating tetraploid seeds is twice, and catalase activity more than twice that in diploid seeds (126). During most of the growing period, assimilation is greater in the diploid than in the tetraploid (169), and since the growth rate of the diploid is also greater, the greater size of the tetraploid (or certain parts thereof) seems to be attributable to the large size of the cells and to the increased number of culms (21, 274). However, Karpechenko (425), Freisleben (227) and Müntzing (559) found that some tetraploid races had fewer culms than parental diploids. Chen (126) noted that reduction of methylene blue by extracts from $2n$ leaves was more rapid than from $4n$ leaves. Fruiting is delayed in some (124, 559) but not other (423) tetraploids. The time between opening and closing of the florets at anthesis is longer in autotetraploids (425).

A colchicine-induced autotetraploid of White Winter was less winter-hardy than the parental diploid form (772). However, the osmotic pressure value of the sap of leaves was about 10% higher in a tetraploid than in the parent diploid strain (21, 227). Greis (274), on the other hand, reported a lower cell-sap concentration in the autotetraploid as compared with the parental diploid.

Smith (727, 728) reported that autotetraploid Everest survived heavier treatments of X-rays than diploid Everest, but the diploid possibly had greater tolerance for high temperature treatments. The frequency of bridges per cell in root tips grown from irradiated seeds given 10,000r was 2.0 for the autotetraploid and 1.0 for the diploid. Heat treatment of seeds (80° C. for one hour) had little if any effect on the frequency of chromatinic bridges in either diploid or tetraploid. Tetraploid seeds had a slightly higher moisture content. Müntzing (555) found no appreciable difference in the moisture content of seeds of diploid and tetraploid Opal.

Müntzing (555) found that germination, vigor and fertility of autotetraploid Opal were reduced less by X-raying than in the diploid line. No mutants were noted in an X_2 of 2,365 tetraploid plants, while 75 mutants were present among 5,483 individuals from the diploid (557). The differences between the diploid and autotetraploid lines were accounted for on the basis of gene and chromosome duplication.

Levan (488) showed that diploids and autotetraploids had about the same thresholds for reaction to colchicine, as measured by mitoses and tumors.

Another difference between diploids and autotetraploids, including those of barley, that is presumably based on physiological differences, is that they usually exhibit changed responses to hybridization. Autotetraploids of some species have been successfully used in interspecific and intergeneric crosses where crosses with the diploids failed. In barley, crosses between tetraploids and parental diploids have rarely if ever been successful [8]. Freisleben (reported by Lein, 478) obtained a viable seed in crosses between a tetraploid race of *H. bulbosum* and autotetraploid cultivated barley, but the seedling died. He was unable to obtain viable seeds in crosses between the 4*n* *H. bulbosum* and diploid cultivated barleys. Attempts to cross autotetraploid barley with wheat failed (423).

Autotetraploid barleys are more susceptible to ergot than diploids (425). The writer [9] has observed the same to be true with autotetraploid rye and with a considerable number of male sterile and meiotically irregular mutants in einkorn. Thus he would be inclined to attribute the greater number of ergot sclerotia in autotetraploid barley and rye to the higher frequency of sterile florets rather than to changes in physiology. Vavilov (853) likewise noted a correlation between sterility and number of ergots.

Meiosis in autotetraploid barley is irregular, with more or less random pairing among the four homologs (124, 227, 610, 679). The usual number of quadrivalents at first metaphase is one to three, but the maximum of seven has been observed. Other ir-

[8] Unpublished observations of H. V. Harlan, M. L. Martini, H. Stevens, and G. A. Wiebe. Tsuchiya (1949A) recently reported crossing tetraploid Golden Melon with a normal diploid plant. (See section on Triploids.)

[9] Unpublished observations.

regularities are autosyndetic associations involving more than four chromosomes, univalents, trivalents, bridges and evidence of structural change (124, 227, 423, 679). Peto (610) examined diploid and tetraploid florets on the same spike and found 1.87 times as many chiasmata in the autotetraploid as in the diploid pollen mother cells. Rosendahl (679) observed no distinct difference between "F_1" and "F_2" tetraploid plants in frequencies of bivalents, trivalents, etc. There was an average of 0.78 chiasmata per chromosome.

One heat-induced autotetraploid was a hybrid between a six-rowed winter and a two-rowed spring barley (559). Segregation in the progeny of this plant was complicated.

Meiosis in the tetraploid form of *H. bulbosum* is similar to that in autotetraploids of *H. vulgare,* indicating that the form is autotetraploid (59, 128, 129, 478). Berg (59) presented diagrams of various types of configurations, with data on frequencies. Of 734 quadrivalents, nearly 90% of them were arranged so that adjacent chromosomes would disjoin at first meiotic anaphase. Chin (129) reported similar results on a smaller population of microsporocytes.

The irregular meiosis in autotetraploids of cultivated barley results in $2n$ and $4n$ pollen in the same anther, hypo- and hypertetraploid progeny (124, 161, 423, 561, 679, 725), and diploids with reduced fertility. Müntzing (555, 559) estimated that about 50% of the progeny of autotetraploids had aberrant chromosome numbers. Karpechenko (423) found that 19 of 22 "F_2" plants had 28, two had 29, and one had 27 chromosomes. Rosendahl (679) studied 18 crosses among two autotetraploid races and observed one "F_3" plant with $2n = 24$, and another with $2n = 30$ chromosomes, that produced seeds. F_2 plants with 25 to 31 chromosomes were found. The degree of pollen sterility was not a reliable index of meiotic irregularity but was fairly closely correlated with seed setting. Chen et al. (124) found some autotetraploid plants that seemed regularly to have 14 pairs of chromosomes.

Müntzing (556, 558, 559) tested autotetraploids with a view to their practical usefulness. He observed obvious differences in vigor, fertility and frequency of aberrants between strains. The grain yield of ten tetraploids ranged from 21 to 54% (averaging

40%) of the yield of corresponding diploids. Best yields were obtained from selections in the offspring of crosses. Some selections yielded about 80% as much as the diploids. Belief was expressed that this difference could be decreased. Similar optimism was expressed by Ono (590) from a study of 20 colchicine-induced tetraploid strains, some of which had up to 85% fertility in later generations.

ANEUPLOID AND STRUCTURAL VARIATIONS

TRISOMICS. Trisomic plants of barley have been described by Katterman (430) and Smith (725). Both investigators studied meiosis in $2n + 1$ plants, which was similar to meiosis in trisomics of other genera. Stählin (747) apparently found a trisomic plant from a root-tip count of chromosomes in *H. distichum*.

INTERCHANGES. Several workers (118, 308, 408, 725, 731a, 733, 868) have studied interchanges in barley. Some have been spontaneous (408, 725, 733); others have resulted from irradiation of pollen [10] or seeds (118, 308, 731a, 868, 886).

Quadrivalents in one heterozygous interchange (725) were so oriented that at first meiotic anaphase 60% of the (classified) cells would have disjunction of alternate chromosomes. Fertility of three ring-forming plants (65–69%) was a little higher than expected on the basis of meiotic configurations if it is assumed that disjunction of adjacent chromosomes results in potentially viable spores. Burnham (118) and White and Burnham (886) observed that in 27 different interchange heterozygote stocks, the pollen abortion varied from 15 to 40%; whereas one line with two separate rings of four had about 51% aborted pollen. Ovule sterility in plants with one ring of four varied from 25 to 92% (118). There was no close correlation between pollen and ovule sterility. The one plant with two rings of four had 67% seed sterility. Smith (733) likewise found that plants with a ring of four chromosomes had about 28% pollen and ovule sterility. He observed that only about 12% instead of the expected 50% of 261 F_2 plants from a cross involving one interchange were partially sterile, i.e., received the interchanged chromosomes. Hanson and Kramer (308) observed that ovule sterility in normal plants ranged from

[10] Author, unpublished observations.

1 to 13% with a modal class of 1 to 2%. Progenies of plants heterozygous for an interchange had modal classes of 1 to 2% and 23 to 24% sterility, indicating that the interchanges resulted in about 23% ovule abortion. It has been pointed out (308, 731), however, that the degree of sterility would be expected to vary in different interchanges, depending upon the manner of segregation and the frequency of crossing-over between the centromere and the point of interchange.

As related earlier under Autotetraploids, about 90% of the quadrivalents in autotetraploid *H. bulbosum* were arranged in "zigzag" configurations (59, 129).

Joachim (408) outlined a method for determining the linkage relations between an interchange identified by partial sterility and a gene giving a 3:1 ratio in F_2. One interchange was found to be linked with v (Group 1) with a recombination value of 7%. The other chromosome pair involved was not identified. Waddoups (868), using the same methods in a study of several interchanges, associated one interchange with Linkage Groups 3 and 5 and another with Linkage Group 4. Smith (733) found complete linkage between an interchange and the ms factor, but ms has not been located in any linkage group. Hanson and Kramer (308) found one interchange linked with genes in Linkage Groups I and IV; another was linked with Group IV, but the other chromosome was not identified.

INVERSIONS. Smith (725) reported bridges and fragments at microsporogenesis in a partially sterile stock, and interpreted the aberrations as resulting from crossing over in a heterozygous inversion. Fertility was not reduced so much as expected on the basis of cytological observations. It was pointed out that workers studying other organisms have accounted for this phenomenon by suggesting that noncrossover (viable) chromatids usually get into egg nuclei as a result of orientation of the chromosomes.

(To Be Continued in the March Issue)

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